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DYNAMICS

OF THE DENSE MOIST EVERGREEN FORESTS

LONG TERM MONITORING

OF AN EXPERIMENTAL STATION

IN KODAGU DISTRICT (KARNATAKA, INDIA)

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Abstract

This working paper reviews the various research activities undertaken in a permanent experimental field station near Uppangala village at the foot of the western slope of the Western Ghats. Three forest compartments, all situated in a low-elevation moist evergreen dense forest type dominated by dipterocarps, are being monitored since the mid-80s and early 90s.

Different types of research projects are being carried out in these compartments on: the impact of selective logging on forest composition, structure and dynamics; the forest structure and diversity and their local variation in relation to topography and silvigenesis; tree architecture and growth; phenology and litterfall; relationships between forest composition and pollen rain; impact of human activities on the vegetation around the village.

This station thus provides a common field for new methodological developments and for various ecological and socio-ecological studies.

Key words: rain forest, permanent plot, forest dynamics, silvigenesis, biodiversity, structure, phenology, litterfall, logging.

Résumé

Ce document de travail décrit les recherches menées dans une station expérimentale de terrain permanente située près du village d'Uppangala, au pied du versant ouest des Ghats occidentaux. Trois parcelles, appartenant au type des forêts denses humides sempervirentes de basse altitude et dominées par des diptérocarpacées, y sont suivies depuis le milieu des années 80 et le début des années 90.

Différentes études y ont été, ou y sont encore, réalisées. Elles portent sur : les variations de composition et de structure en relation avec la topographie et les mécanismes de la sylvigenèse; l'architecture et la croissance des arbres ; la phénologie et la chute de litière ; les relations entre composition floristique et la pluie pollinique; l'impact de 1'exploitation forestière sélective sur la composition, la structure et la dynamique de la forêt; l'impact des activités humaines sur la végétation à proximité du village.

Cette station sert ainsi de support à des travaux méthodologiques et fournit un terrain commun pour des études d'écologie et de socio-écologie.

Mots-clés : forêt dense humide, placette permanente, dynamique forestière, sylvigenèse, structure, biodiversité, phénologie, chute de litière, exploitation.

Context and objectives

In 1984, the Kadamakal Reserve Forest, near the Uppangala village, was selected to set up a permanent experimental station with the general aim to study and compare the functioning and dynamics of logged and unlogged dense moist evergreen forests dominated by Dipterocarpaceae in the Western Ghats[1].

The basic scientific objectives were, and still are: the analysis of the forest mosaic and its renewal, the description and comprehension of the mechanisms of silvigenesis, the quantification of the response of the stands to moderate disturbance regimes (selective felling). The expected applied outputs should help in the formulation of management guidelines for these original formations which contain a large number of endemic species {*i.e.* about 60% of tree species present in the Western Ghats are endemic), but whose survival is threatened by human pressure which is very strong in Southwest India (Buchy, 1990, 1996; Garrigues *et ai,* 1993). This station also serves as a support for several other specific studies, such as to establish relationships between the forest composition and the pollen spectra which are observed in the palynological studies on the history of the South Indian vegetation that are carried out by the French Institute (Anupama, 1996).

The primary aim of this paper is thus to provide an overview of the various studies carried out in the so-called "Uppangala station": of the monitoring design and methods, as well as of the first results and perspectives. Readers interested in more detailed information are invited to consult the papers referenced in the last section. Another more general objective is to illustrate the role and importance of such permanent plots and experimental sites, which serve as open-field laboratories where scientists and students follow each other over the years, cross disciplines and viewpoints, progressively accumulating data, developing new methods and refining theories that will ultimately be tested and used by their successors.

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1 The main partners involved in the management and scientific studies of this permanent site are: the Kamataka Forest Department (KFD) which manages the Kadamakal Reserve Forest and has given the authorization for entering the forest; the *lnstitut français de Pondichery,* which framed the sampling design and has been monitoring the station through regular surveys completed by special measurements performed by students and scientists for specific studies; the *Laboratoire de biométrie, génétique et biologie des populations (CNRS-UMR 5558)* at University of Lyon I: since its inception, Dr. J.-P. Pascal has been holding the scientific responsability of the station; the Salim Ali School of Ecology and Environmental Sciences at the Pondicherry University: several students participated to studies on this site.

Location and design of the experimental station

The experimental station is situated in the Kadamakal Reserve Forest (Kodagu District), near Uppangala a small village (less than 20 houses and 100 people), in the foothills of the Ghats (12°30' N, 75°39' E). Annual rainfall is about 5200 mm with a marked dry season of 3-4 months. The experimental station itself is located at an altitude comprised between 400 and 600 m.

The natural vegetation belongs to the *Dipterocarpus indicus - Kingiodendron pinnatum - Humboldtia brunonis* type of low elevation moist evergreen forests described by Pascal (1988). Although more than hundred species have been observed in the forest itself, it is less rich and diverse than other tropical rain forests in South East Asia or South America. Half of the species present in the Kadamakal Reserve Forest are endemic to the Western Ghats and about 80% of the trees belong to these endemic species (Pascal & Pélissier, 1996).

This forest is remote — the gravel road to Uppangala village is a dead end and was created after 1959 — and situated at the very foot of the steep western slope of the Ghats, so that it has been relatively well protected from human impacts. Harvesting only began in 1974 and was stopped in 1988 when Karnataka decided to impose a general felling ban (Loffeier, 1989). It thus turns out that the compartments have either been logged only once or were never harvested.

The experimental station itself contains three compartments:

- a network of 8 plots of 600 m^2 each, surveyed in 1987-88 in a "control" compartment which had never been harvested;
- a network of 14 plots of 600 m^2 each, first measured in 1985 and 1986 in a 28 ha compartment which had been selectively exploited 6 years earlier (8.5 trees felled per ha, logs being hauled by elephants) and which had then partly burnt (Fig. 1);
- a 28 hectare undisturbed compartment monitored since 1990, and sampled using three complementary systems (Fig. 2): five transects aimed at ensuring statistical representativity of the compartment, three plots dedicated to the study of the forest mosaic, and four other plots for the specific study of *chablis (i.e.* tree fall gaps). Thus, more than 5 ha have been extensively studied.

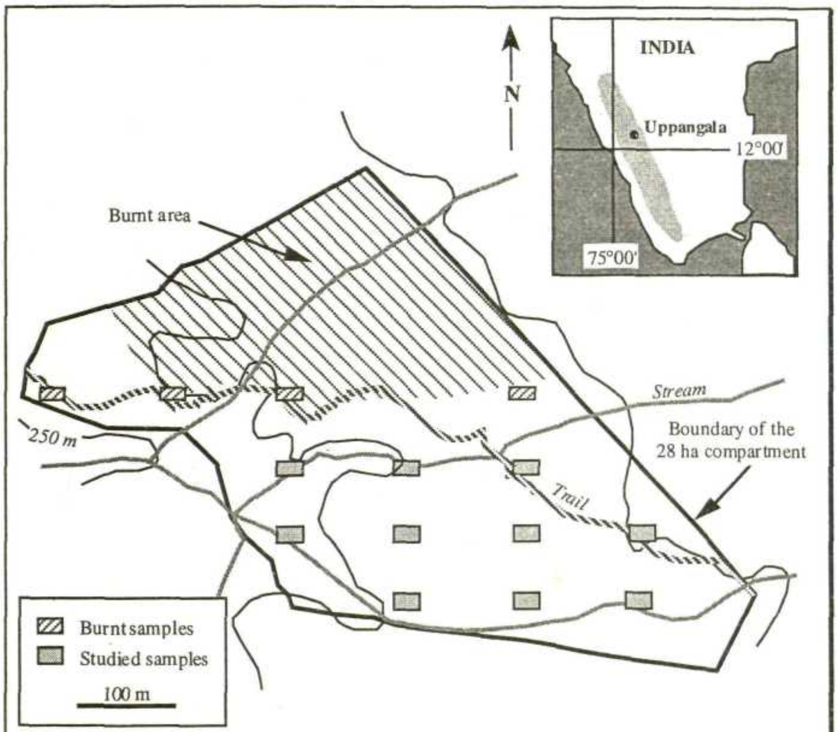

Figure 1. Sampling design in the once-logged 28 ha compartment (from Pélissier *et al.*, in preparation).

Sample plots have an area of 600 m² (30x20 m). All plots were surveyed in 1985-86. Only the unburnt plots were remeasured in 1987-88 and 1992-93.

Canopy cover is open in the burnt area: it is dominated by a few remaining large trees and has been colonised by *Macaranga peltata*, a light-demanding pioneer species.

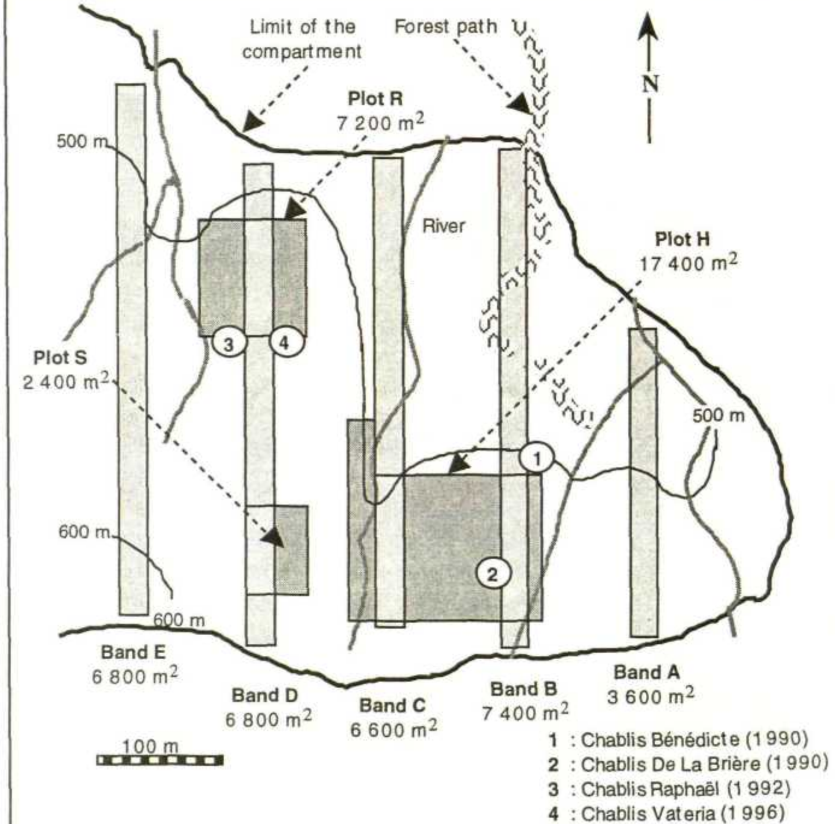

Figure 2. Sampling design in the 28 ha undisturbed compartment (from Pélissier, 1995).

The five transects (bands A to E) are aimed at providing a good statistical representativity of the whole site: characterisation of the girth structure of the stands, evaluation of species diversity, biometric assessment of the dynamics of the stand (growth, mortality and recruitment).

The three rectangular plots (H, R and S) were set up to characterise the forest mosaic and its functioning in three topographic situations where the physiognomy of the stand is very different from each another.

Finally, four small plots (1, 2, 3 and 4) were established in gaps resulting from chablis, in order to study the way in which a stand evolves following a more or less large opening in the canopy.

Measurements and data

In the three compartments, trees with girth exceeding 30 cm were spatially located and botanically identified at the species level. Further, a subsample of saplings higher than 2 m high were also located, identified and measured.

The network of 14 plots located in the disturbed forest was surveyed three times, in 1985-86, 1987-88 and 1992-93. The measurements recorded were:

- girth at 1.30 m (gbh) of trees with gbh>10 cm,
- total height, spread and length of the crown of trees with gbh> 10 cm (such data rarely available in tropical rain forests);
- total height of saplings at least 2 m high.

The network of 8 plots in the control undisturbed compartment was surveyed only once, in 1987-88, when gbh was measured.

Since 1990, the French Institute has been systematically monitoring the undisturbed 28 ha compartment, with a semestrial — until 1995, when it became annual — inventory of gbh: measurements being recorded by micro-dendrometers fixed on about 5700 trees with gbh>30 cm. The height of saplings (more than 2 m tall) was also monitored in some plots.

Other observations and measurements made in this compartment were:

- topography mapping;
- light measurements (in 1990 and 1993) and description of crowns in the three plots devoted to the study of the forest mosaic (in 1992);
- from January 1991 to December 1994, monthly measurements of litterfall (systematic sampling of 100 baskets over one hectare);
- from December 1992 to December 1994, monthly follow-up of the phenology of about 500 trees (representative of the 91 species present in the plot): flowering, fruiting, leaf and shoot flushes;
- atmospheric pollens were also studied using traps, soil surface samples and spider webs;
- monitoring of seedlings and saplings in treefall gaps: three plots have been surveyed twice (in 1990 or 1992, and in 1996) while the most recent chablis has been inventoried only once (in 1996).

Database and data analysis

The data are entered into a relational database which is regularly updated (Fig. 3). For an automatic 3-dimensional representation of tree morphology and stand physiognomy, a specific software was first developed (in Pascal language on Macintosh) by Loffeier (1989) and then taken up again by Pélissier (1995; see Fig. 4 for an illustration).

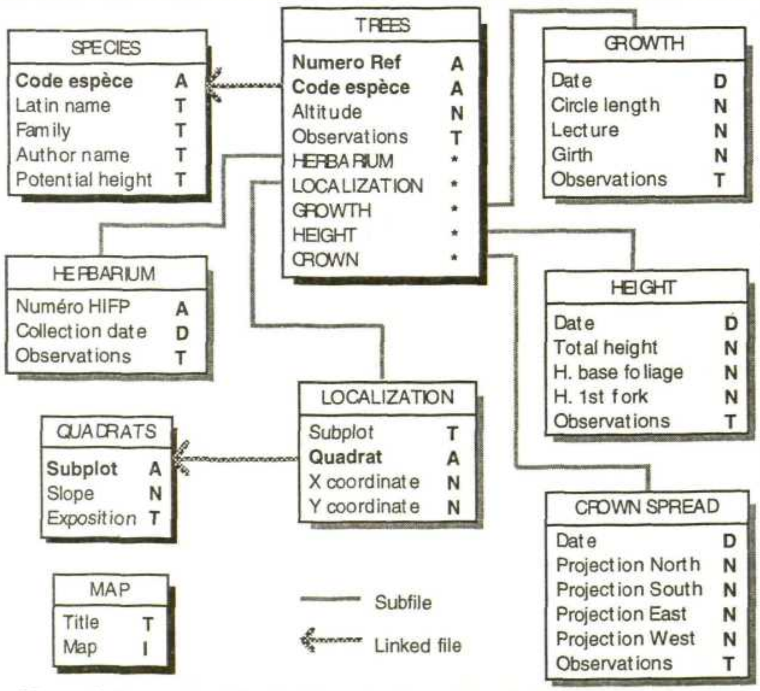

Figure 3. Structure of the database for the undisturbed compartment (from Pélissier, 1995).

The database was implemented using 4ème Dimension for Apple Macintosh. A: key attribute; D: date; N: numeric value; T: text.

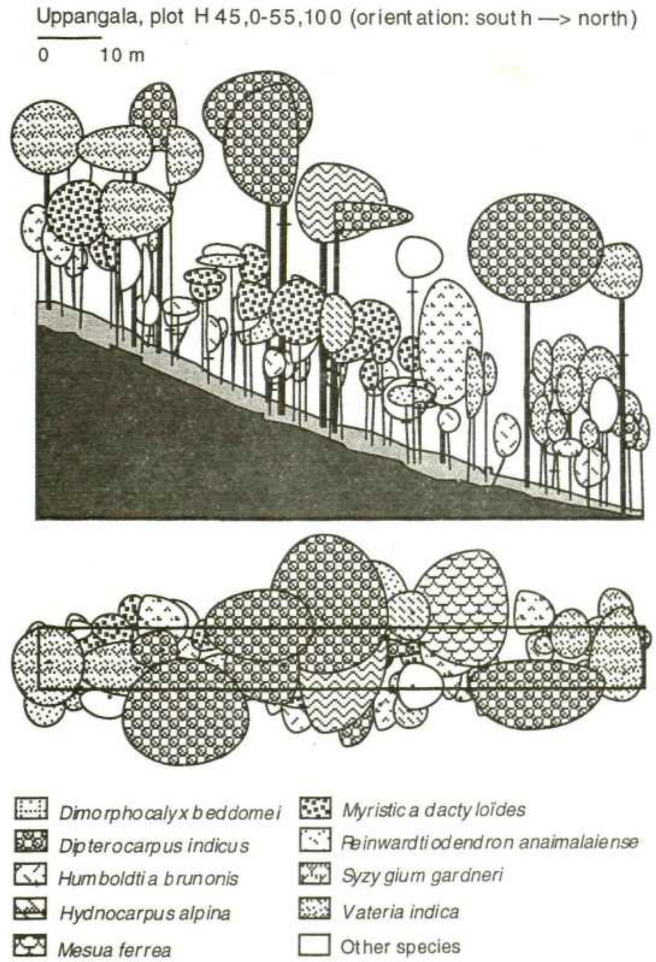

Figure 4. Physiognomy of an undisturbed forest plot on a gentle slope (from Pélissier, 1995).

Classical statistical methods — namely analysis of variance, regression and multivariate analyses — were applied to describe the size *vs.* species structure of the forest, to classify the species into functional groups, to analyse the height *vs.* diameter relationship, to model growth as a function of diameter, species and competition (Loffeier, 1988, 1989; Pélissier, 1995; Pascal & Pélissier, 1996).

Different designs were simulated in order to select a suitable sampling strategy (comparison of simple random sampling, systematic cluster sampling and stratified cluster sampling) for estimating tree species richness and α-diversity in the moist evergreen forests of the Western Ghats (Gimaret *et al.,* 1996).

Using methods derived from the theory of point processes and based on the analysis of the distribution of distances between trees (see Ripley, 1981), specific programmes were developed for analysing the spatial structure of the stand (Pélissier, 1995).

Main results

Forest dynamics and impact of logging

First results by Loffeier (1989) showed that undisturbed forests in the Western Ghats have a relatively high basal area (*ca.* 40-55 $m^2.ha^{-1}$) as compared to other tropical moist evergreen forests. Loffeier also demonstrated that selective felling of about 10 big trees per hectare does not greatly alter the structure and functioning of the forest on the short term. He built an average growth model for two commercially and ecologically important species, *Vateria indica* and *Dipterocarpus indicus,* and estimated their minimum felling age (*i.e.,* time before reaching a dbh of 60 cm): about 120 years for *V. indica* and 200 years for *D. indicus.* He also outlined a simple demographic model which helped him proposing some management guidelines: the minimum rotation between two successive moderate selective harvesting should be more than 30-40 years in order to let the forest recover, not only in terms of biomass but also of stand structure and composition.

Loffeier further suggested that in these forests of the Western Ghats, silvigenesis by substitution (*i.e.,* the "identical" replacement of a standing tree by one of his neighbours which was till then its subordinate) is a mechanism which is at least as important as silvigenesis by chablis. Curtet (1993) and Pascal (1995) then made a detailed analysis of situations where this substitution mechanism may occur.

A biometric appraisal made after 7 years provided complementary information on the reconstitution of the stand after selective exploitation (Cousin & Voyez, 1993). About ten years after harvesting: the frequency of light-demanding pioneer species, which had colonised the large openings, has sharply diminished; the net change in basal area remains positive at +0.56 $m^2.ha^{-1}.yr^{-1}$; the inter- and infra-specific variability in individual diameter increment is very high.

This work was then completed by a comparative study in the 28 ha undisturbed compartment (Laborde, 1994; Pélissier *et al.,* in preparation). This study *(i)* confirmed that a single low-damage — logs were hauled by elephants — selective exploitation does not deeply alter the forest structure, diversity and that the recovery in biomass and basal area is fairly rapid (Table 1) with a strong stimulation of individual growth (Fig. 5), *(ii)* but suggested that the repetition of such harvesting might have a strong long term impact on the forest composition and dynamics: the commercially interesting emergent and upper canopy species being replaced by understorey species.

Table 1. Density and basal area balance in the undisturbed and once-logged compartments. Minimum dbh=10 cm (from Pélissier *et al.*, in preparation).

	Initial state (ha^{-1})	Final state (ha^{-1})	Mortality ($ha^{-1}.yr^{-1}$)	Recruit-ment ($ha^{-1}.yr^{-1}$)	Growth ($ha^{-1}.yr^{-1}$)	Balance ($\%-yr^{-1}$)
Once-logged compartment A - Sampled area: 0.6 ha - Period: 1986-1993						
Density (stems)	578	617	5.0	10.5	-	+0.95
Basal area(m^2)	34.8	38.8	0.40	0.10	0.86	+1.61
Unlogged compartment B - Sampled area: 3.12 ha - Period: 1990-1994						
Density (stems)	606	619	5.2	8.5	-	+0.54
Basal area(m^2)	39.3	41.0	0.26	0.07	0.59	+1.02

Note: mortality and recruitment were assessed once, at the end of the period of study.

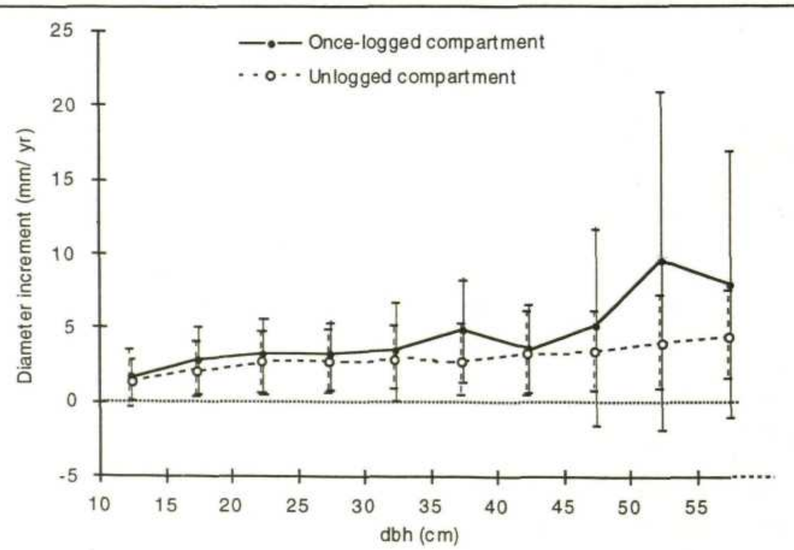

Figure 5. Stimulation of individual diameter increment due to logging. Mean and standard deviation of the annual diameter increment in relation to diameter at breast height (dbh) in the undisturbed (1990-94 period) and once-logged (1986-93 period) compartments (from Pélissier *et al.*, in preparation).

Forest structure and diversity

Derouet (1994) and Pascal & Pélissier (1996) defined groups of species which have similar diametric structure which correspond to distinct ecological behaviours and functions in forest dynamics. They also showed that these forests certainly have a high species richness — 40-60 tree species per hectare and more than 100 species in the 28 ha undisturbed compartment —, but that only a few species constitute their framework: two Dipterocarps, *Vateria indica* and *Dipterocarpus indicus,* one Fabaceae, *Humboldtia brunonis,* and two Myristicaceae, *Knema attenuata* and *Myristica dactyloides,* represent more than 50% of the biomass and number of individuals. The Clusiaceae are another important family.

The systematic sample in the 28 ha undisturbed compartment was used by Gimaret *etal.* (1996) to test different sampling strategies for estimating tree species richness and α-diversity. They demonstrated that several hundred of individuals sampled in small clusters —say 20 plots distributed along a square 100 m x 100 m tract, each plot with 20 sample trees, that is a total number of 400 trees — are enough to estimate species richness and diversity (as evaluated using Simpson index). They also tested several non parametric estimators of species richness and empirically verified that they provide much better estimates than the usual number of observed species. This strategy was then applied in other forest ecosystems and agrosystems *(e.g.* coffee plantations; see Pommery (de), 1996) with the aim to assess changes in species richness diversity along bioclimatic and disturbance gradients.

Pélissier (1995) mainly focused on the spatial analysis of the forest mosaic in the 28 ha undisturbed plot, and provided a new insight into the relationships between local environmental factors, the structure and the dynamics of the stand. By combining graphic representations (*e.g.* Fig. 4) and statistical analysis of the distance between trees, he indeed demonstrated that different patterns of spatial structures (vertical and horizontal) exist and that they are associated with different topographical situations and, most probably, with different types of forest dynamics:

- on the slopes, the forest is more heterogeneous and diverse (Gimaret, 1995; Gimaret *et al.,* 1996), with *chablis* and gaps playing a major role;
- while forest is less diverse, but denser and more regular on crests and plateaux, with substitution playing a key role in silvigenesis (Pascal, 1995).

Several other ecological studies have been realised: on the organisation and diversity of ant communities (Basu, 1994) and fish communities (Ramakrishnan 1989), and on the dissemination of some forest tree species (Sinha, 1990; Sinha & Davidar, 1992).

Uppangala as a village in the forest

Salaün (1995, 1996) did not focus on the forest itself, but on Uppangala village, people and their relationships with the forest. In fact, she carried out a comparative ethnobotanical study of four village communities living in forests, one of them being Uppangala: she investigated the effect of human activities on the surrounding vegetation and analysed how the villagers perceive and use the forest and plants, and how they organise the space within and around the village.

Robert & Salaün (1996) further mapped Uppangala —houses and land use — and analysed its spatial structure and dynamics. They pointed to the changes occurring in such a small village enclosed into the forest and at the end of the road: being officially barred by the Forest Department from extending fields into the forest, the people resort to a strategy which combines low-profile but steady encroachment upon forest to continuous adaptation of farming systems within the village, shifting from traditional farming to cash crops *(e.g.,* paddy fields are replaced by arecanut plantations).

The output of these processes is not spectacular — there is no clear-cut area and Uppangala cannot be termed a pioneer front—, but the changes in the landscape and forest ecosystems are real and deep though gradual: for example, in the immediate vicinity of the village, the original moist evergreen forest has been replaced by secondary moist semi-evergreen forest.

Perspectives and ongoing studies

Tree architecture

The analysis of tree architecture of some species began in 1995 in collaboration with the *Unité de modélisation* at CIRAD[2], Montpellier. The ultimate objective is to simulate the 3-dimensional dynamics of a rain forest in order to improve our understanding of silvigenesis, stand functioning and stand reaction to disturbance. One central problem is thus to describe and model the way in which the trees occupy space and some aspects of their interactions (competition by contact and for light)[3].

The study focuses on a few species which constitute the framework of the forest and play different roles in its functioning: *Dipterocarpus indicus* (Dipterocarpaceae, an emergent species), *Vateria indica* (Dipterocarpaceae, an emergent/upper canopy species), *Knema attenuata* (Myristicaceae, a lower canopy species), *Humboldtia brunonis* (Fabaceae, an understorey species) and, later on, *Macaranga peltata* (Euphorbiaceae, a light-demanding pioneer species). It is based on several steps: a qualitative description of tree architecture, quantitative measurements of the stem and branches (size, length, number of internodes per growth unit), statistical modelling and finally computer simulation (Houllier *et al.,* 1997; Durand, 1997).

Preliminary results show that light availability has a strong influence on the architectural development of *V. indica:* not only on the growth rate of the seedlings and saplings, but also on the probability of death of the apical meristem when the tree is young — and thus on the edification of the stem —, and on the metamorphosis of the upper branches when they reach the upper canopy (Durand, 1997; Durand *et al.,* 1995).

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[2] CIRAD: Centre international de coopération en recherche agronomique pour le développement.
[3] It hence appears that certain differences in the forest functioning observed between India and French Guyana are attributable, among others, to differences in tree architecture (B. Riéra, *pers. comm.).*

Forest dynamics

From the biometric assessment of forest dynamics in the undisturbed and logged compartments (Pélissier *et al.,* in preparation), it is now intended to develop a matrix demographic model of the dynamics of tree populations (Favrichon, 1995). Species will be aggregated into a few functional groups which are composed of species that have similar demographic traits (growth, mortality and regeneration). The model will also include spatial constraints and features — such as density-dependence of growth, mortality and recruitment or dispersal of species —, which play a key role in the regulation of population dynamics.

A third approach of forest dynamics was initiated by Moravie (1995; see also Pascal *et al.,* 1995), with the aim to model tree growth and forest dynamics. This approach is intermediate between the detailed architectural description and global demographic models. It consists in a two-dimensional cellular automaton which is driven by the expansion of crowns which is itself constrained by competition; stem diameter increment is then predicted from crown growth (additional information on tree height growth is provided from height *vs.* diameter allometric curve). This automaton also requires information on two other processes which are more difficult to model: the mortality and regeneration.

New field studies are thus being started in order to analyse these processes. The changes in structure and composition of seedlings and saplings are being monitored in gaps that were first studied and mapped in 1990, 1992 and 1996 (Fig. 2). A preliminary study of the soil seed bank (Santosh, 1996) has yielded interesting but surprising results: the seed bank is nearly empty, which suggests that the regeneration is heavily dependent on the simultaneity of fruiting and opportunities, such as the creation of gaps or small openings either due to chablis or to the death of a standing tree.

The analysis of rare events such as cyclones and windstorms would most probably help in understanding the long-term dynamics of these forests. Such events are hence likely to play an important role in the renewal of these forests, which exhibit in some places a fairly regularised structure (with a homogenous high canopy and a low understorey, but with only a few intermediate trees). This type of study is always difficult and can only be made when a longer series of data is available or thanks to a comparative approach including many sites.

As a first step, an exhaustive survey of standing and fallen dead trees was carried out in 1996 by M.-A. Moravie in the undisturbed compartment. All species pooled together, the annual mortality rate was estimated at 0.86 $\%.yr^{-1}$, with no clear difference among size classes. A joint analysis of mortality and prior girth increment showed that the increment had decreased before the trees actually died. The spatial distribution of mortality was analysed using Ripley's methods: - there is an aggregation at short distance, whichever the cause of mortality is;

- the primary and secondary *chablis* are at an average distance of at least 12 m;
- primary *chablis* and dead standing trees are regularly distributed (with an approximate distance of 40 m).

Phenology, aeropalynology and litterfall

A preliminary report on the phenological data obtained over the last two years was prepared (Aravajy, 1995). This study will serve as the basis for *(i)* orienting more detailed investigations of phenology, seed dispersal and regeneration, *(ii)* analysing tree architecture (see above), and (*iii*) providing insights in litterfall and aeropalynological studies (see below).

The first analysis of the phenology of four species belonging to different forest strata — *Dipterocarpus indicus, Vateria indica, Knema attenuata, Humboldtia brunonis* — showed sharp differences in the behaviour among the species (Aravajy *et al.,* in preparation). The flowering and fruiting of the two dipterocarp species start when they reach the canopy: as observed for many species of this family, they exhibit irregular flowering and fruiting patterns; although *D. indicus* produces a few fruits every year, mass-fruiting happens only every few years, a strategy that is more pronounced for *V. indica*. *K. attenuata*'s flowering starts before the tree reaches the canopy level and lasts for several months, a strategy which helps this species to reproduce itself as early as possible. *K. attenuata* is a dioicious species, flowering each year during a long period, which is longer for male than for female flowers.

After preliminary studies carried out by Dario de Franceschi and Tissot & Caratini (1994), different types of samples — aerial filters, superficial layer of the soil, spider webs, honeycombs — were collected in 1996, with the aim to study the relationship between the pollen rain and the floristic composition of the forest. Preliminary results confirm that there is a high distortion between forest composition and airborne as well as soil pollen spectra (Anupama, 1996), a result which has important consequences for paleopalynological studies.

Litterfall data collected from 1991 to 1994 are being analysed (B. Ferry, in preparation) with the aim: (*i*) to estimate the primary production of the undisturbed forest with reference to other Indian forests and bioclimatic gradients; (*ii*) to analyse the temporal variation and spatial pattern of litterfall and compare them with the inter- and infra-annual climatic variations, and the spatial distribution of the trees; *(iii)* to assess the rate of litterfall decomposition.

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